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A SAMPLING METHOD TO ASSESS LOTIC CRAYFISH COMMUNITIES

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ABSTRACT

Crayfish are widely recognized as an important ecological component of stream systems, but there has been limited work to develop and evaluate the reliability of sampling methods for lotic crayfishes, especially efforts that are temporally and spatially comprehensive. We desired a quantitative method to assess crayfish communities in streams with rocky substrate. Our objective was to develop a method to obtain and compare representative density estimates with acceptable variance and reasonable effort, and to illustrate use of the method by using it to 1) describe and compare diurnal habitat associations by lotic crayfish, and 2) detect density changes over time. Our study encompassed four sites on two rivers, two seasons, and 8 y (1991–1998) to evaluate a 1-m^2 quadrat sampler, and a sampling method that stratified effort among five macrohabitats to reduce variability. This method performed well for both seasons, detecting spatial differences among macrohabitats and temporal differences among years. Spatial differences were expressed as macrohabitat selectivity by the crayfish community, and showed a consistent trend across streams and seasons. In particular, macrohabitats with slower current velocities consistently had the highest densities. Temporal differences included documentation of decreased densities in several macrohabitats across 5 y. Sampling precision, measured by coefficients of variation, was acceptable but not considered high. Statistical power was good for detecting spatial differences, but reduced and variable for detecting temporal changes. Our findings 1) demonstrate the use of stratifying quantitative sampling for lotic crayfish communities by habitats, 2) confirm the importance of evaluating sampling methods, and 3) illustrate the consistent way in which Ozarks crayfish communities used available macrohabitats.

Crayfish are widely recognized as an important ecological component of stream systems. They process organic matter, transfer energy between trophic levels and affect the structure of benthic invertebrate communities (Momot *et al*., 1978; Creed, 1994; Momot, 1995; Rabeni *et al*., 1995; Parkyn *et al*., 1997; Whitledge and Rabeni, 1997; Parkyn *et al*., 2001). A variety of gear types and methods has been used to sample crayfishes, but the development of an efficient, reliable method to obtain population or community estimates in streams has been hindered because most gears and methods select for specific life stages, sexes, or species (reviewed in DiStefano, 1993; Rabeni *et al*., 1997). Additionally, crayfishes, like many freshwater benthic macroinvertebrates, typically show spatial heterogeneity or clustered distributions due to factors including habitat preferences (Rabeni, 1985; Skurdal *et al*., 1988), predator-influenced behavior (Stein and Magnuson, 1976; Collins *et al*., 1983), and changing environmental conditions such as temperature (Somers and Green, 1993). Clustered distribution patterns present sampling problems partly because large sample sizes are required to estimate population densities with acceptable precision (Thompson *et al*., 1992). Sample stratification by habitats is commonly used in sampling aquatic biota to address clustered distributions, increase precision, obtain more representative population or community abundance or density estimates (Waters and Erman, 1990; Armitage *et al*., 1995; Rabeni, 1996), and gain a better ecological understanding of the entire community (Rabeni, 2000). However, this sampling technique has rarely been used to improve quantitative estimates of lotic crayfishes, and we found no previous studies that quantitatively evaluated the performance of stratified crayfish sampling in streams or the reliability of the data. We evaluated the performance of a 1-m^2 quadrat sampler

in combination with stratified sampling over a variety of macrohabitats in achieving precise density estimates.

Our primary purpose was to develop and evaluate a reliable (defined as an acceptable level of among-sample variance/precision) quantitative method to obtain and compare, spatially and temporally, diurnal density estimates of stream crayfish communities using a reasonable amount of sampling effort. To evaluate the performance of our quantitative method, we used it to estimate diurnal crayfish community densities and attempted to 1) detect spatial differences in those densities among macrohabitats, and 2) detect temporal density differences across years within those macrohabitats.

Materials and Methods

Study Sites

Our study was conducted on two Missouri (U.S.A.) Ozarks streams, Jacks Fork and Big Piney rivers (Fig. 1). Jacks Fork River is a 6th order, easterly-flowing cool-water tributary to the Current River in southern Missouri, with mean annual discharge of 12.5 $m^3 \cdot s^{-1}$ (Rabeni, 1992). Jacks Fork River flows through the Ozark National Scenic Riverways (U. S. National Park Service). Four species of crayfishes occur in Jacks Fork River, but only three are common: *Orconectes luteus* (Creaser, 1933), *O. ozarkae* Williams, 1952, and *O. punctimanus* (Creaser, 1933). Big Piney River is a 6th order tributary of the Gasconade River that originates in the Ozarks highlands of south-central Missouri and flows north, much of it through pasture land. Big Piney River has mean annual discharge of 15.4 $m^3 \cdot s^{-1}$ (Reed *et al*., 1994). Big Piney River harbors *O. luteus* and *O. punctimanus*. Both rivers are moderately productive (Rabeni *et al*., 1995), spring-fed, contain well-developed riffle and pool sequences, and patches of emergent vegetation, primarily water willow (*Justicia* sp.), are common along shallow margins during the summer. We selected two study sites on each river for autumn sampling and one site per river for summer sampling. Jacks Fork River sites were near Mountain View, Missouri; site 1 was at Ratcliff Ford (U.T.M. zone 15, coordinates 617037E, 4102222N), and site 2 at Blue Spring (U.T.M. zone 15, coordinates 620705E, 4100830N). Big Piney River sites were near Houston, Missouri; site 1 was 0.2 km downstream of Mineral Spring Access (U.T.M. zone 15, coordinates 591459E, 4135928N), and site 2 was 1.0 km downstream of Sand Shoals bridge (U.T.M. zone 15, coordinates 592821E, 4141231N). Sites were between 0.8 and 1.3 km in length, and each contained at least two major pools, three riffles and assorted runs, emergent vegetation patches, and backwater/forewater pools. Jacks Fork River sites had a gradient of about 1.78 $m \cdot km^{-1}$, averaged 0.6 m in depth and 20 to 25 m in width; Big Piney River sites dropped 0.77 $m \cdot km^{-1}$, averaged 0.5 m in depth and 18 to 25 m in width. DiStefano (2000) provided a general description of water chemistry for these streams.

Sample Size Stratification

The 1-m^2 quadrat sampler we evaluated was constructed with a 12-mm angle-iron frame, standing 0.51 m high, and covered on three sides with 2-mm by 3-mm rectangular-mesh netting (Fig. 2). We attached a 1.22-m-long bag made from the same netting on the 4th side (downstream side), and secured bottom flaps made of the same netting on all sides that could be sealed into the substrate to prevent crayfish escape.

We collected 111 samples from selected rivers during a pilot study in 1990 to provide preliminary estimates of among-sample and among-macrohabitat sampling variance (Morin, 1985). Based on the pilot sampling and sample-size determination procedures (Cochran, 1977; Elliot, 1979), we designed a two-step sampling procedure to minimize variability (Downing, 1989) and increase our ability to estimate crayfish densities with a reasonable amount of effort. In the first step, we partitioned a stream into "primary" and "marginal" crayfish habitat based on surface substrate composition. In step two, we partitioned the stream among five common macrohabitat types to stratify sampling effort as suggested by Roell and Orth (1992).

We defined marginal habitat as areas where silt, sand, fine gravel, or bedrock were predominant, and crayfishes were absent or scarce. Sampling on those substrates greatly increased among-sample variance. In contrast, crayfishes were concentrated in primary habitat, containing substrate greater than 16 mm diameter (pebble, cobble, boulder; according to a modified Wentworth scale; Bovee and Milhous, 1978). Both primary and marginal habitat could occur within any of the five macrohabitats identified in the stratification procedure. We restricted our sampling to primary habitat by placing our quadrat only in areas of the stream where a square meter of the surface substrate contained at least some pebble (16–65 mm diameter), cobble (65–250 mm diameter) or boulder (>250 mm diameter). Thus, we eliminated areas where the substrate was comprised totally of silt (0.063 mm diameter), sand (0.06–2 mm diameter), gravel (2–16 mm diameter), and bedrock. Similar strategies were used in previous crayfish studies in lakes to reduce variance and increase precision in results (France *et al*., 1991; Somers and Green, 1993). Intensive mapping of our study sites revealed that marginal habitat composed less than 6% of the total substrate area in our streams, but streams in other regions may contain more extensive marginal habitats.

We used results of a discriminant function analysis (DFA) performed on 83 quadrat samples obtained from marginal habitat at our study sites as a basis for eliminating marginal habitats from our sampling regime (DiStefano, 2000). The DFA quantified our subjective classification of primary *versus* marginal habitats by calculating misclassification rates. A misclassification occurred when an individual marginal habitat sample was misclassified as primary habitat or *vice-versa* in our field sampling as compared to our entire database ($n = 2044$ quadrat samples).

Following elimination of marginal habitat from consideration, we stratified our effort in terms of number of quadrat samples among five macrohabitats (Table 1). Macrohabitats occurred on a scale of 1 m^2 to 1000 m^2 and were not completely discrete (Jowett, 1993). However, current velocity (CV) and depth measurements supported our macrohabitat delineations.

We used a stratified, quadrat-sampling allocation strategy (Scheaffer *et al*., 1990: 109) to estimate crayfish densities at each site. We selected this strategy because it allocated sampling effort based on three important factors: 1) variation (standard deviation) in mean crayfish densities per macrohabitat, 2) the proportional geographic area of each macrohabitat composing the study site, and 3) the cost (time required) of obtaining a sample in each macrohabitat. Analysis of the quadrat data from the pilot study provided

Fig. 1. The state of Missouri, indicating its position within the United States, and the location of study streams, Jacks Fork and Big Piney rivers.

mean crayfish densities for each macrohabitat. Each study site was mapped intensively on two occasions (in two different years) to provide proportional area for each macrohabitat. We used ratios to estimate the cost for sampling each macrohabitat. Riffles, runs, and backwaters required approximately equal effort and were assigned a cost of 1.0. Vegetation patch samples required more time and were assigned a cost value of 1.5. Pool samples generally required the most time (because of depth) and were assigned a cost value of 2.0.

Logistics, time constraints, the number of study sites, and estimates from pilot sampling largely determined the maximum sampling effort (number of quadrat samples) we could expend at each site during an intensive sampling season. We obtained 60–65 samples per site each year, allocated among our five macrohabitats at each site according to Scheaffer *et al*. (1990).

Temporal Considerations

Crayfishes in our study streams were typically nocturnal, seeking shelter in the substrate during the day. This enabled us to sample during the day with little concern for crayfish avoiding the quadrat sampler. We began the study in 1991 with intensive sampling periods ($\geq$ 60 samples per site) in

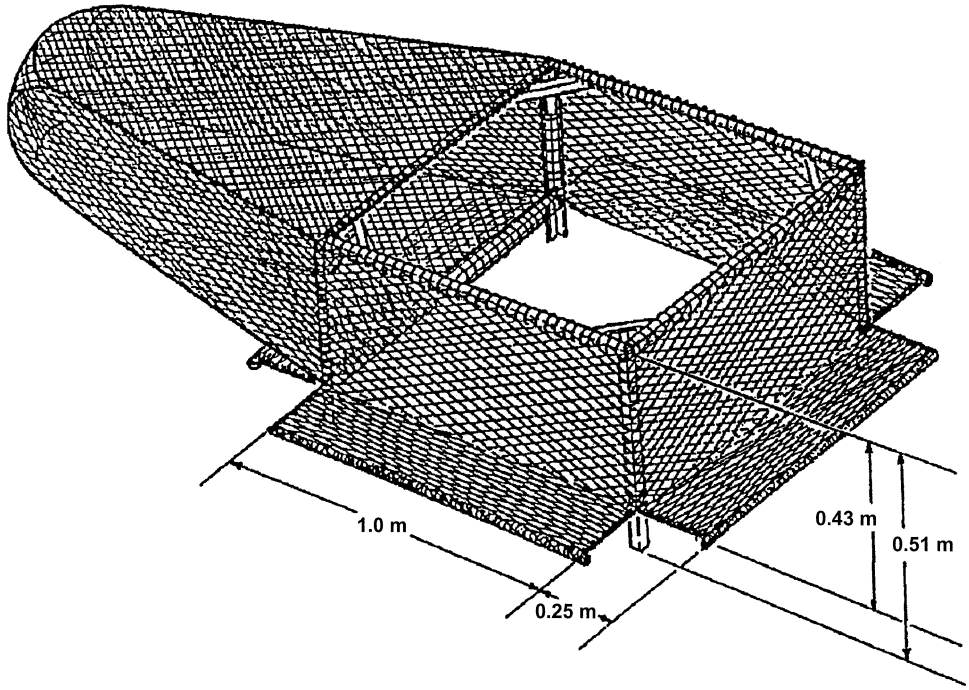

Fig. 2. Illustration of the 1-m^2 quadrat sampler.

late spring (late May/early June) and early autumn (late August/early September) to examine sampling differences between those seasons. We found that spring sampling was unreliable for obtaining density estimates because of high year-to-year variability in timing of recruitment of young. Including these age-0 crayfish in our density estimates was important because they composed numerically more than half of the community (Muck *et al.*, 2002). In 1994, we eliminated spring sampling in favor of an intensive mid-summer (July/early August) sampling period that persisted through the study's completion in autumn 1998. We continued with a less intensive (21 samples per site) early autumn (September) sampling period. Subsequent analysis confirmed that mean crayfish densities for the spring sampling period had higher overall coefficients of variation (105% for Jack Fork River, 93% for Big Piney River) than autumn (70% for Jacks Fork River, 85% for Big Piney River) or mid-summer (82% for Jacks Fork River, 82% for Big Piney River) sampling periods.

Quadrat Sampling Procedure

Quadrat sample locations were not randomized, but rather, systematically interspersed among the range of depths, velocities, and substrate within primary habitat and also within a designated macrohabitat (Hurlbert, 1984). The sampler was sealed into the substrate. We thoroughly disturbed the substrate within the sampler using hand-held garden rakes and our feet for 3–5 min, until we penetrated the substrate to a depth of at least 15 cm. We swept crayfishes downstream by hand into the bag. The quadrat was transported to shore and crayfishes were enumerated and identified. We used SCUBA in deep water (>1.5 m) and snorkeling gear in depths of 0.5 m–1.5 m. In a typical day, we obtained 12 to 20 samples, depending upon the crew size, macrohabitats sampled, water depths, and numbers of crayfishes processed.

Analysis of Quadrat Sampling Data

We analyzed crayfish density data using either 2-way (summer data from only one site per river) or 3-way (autumn data from two sites per river) analysis of variance (ANOVA) to test for differences in diurnal macrohabitat use by the crayfish community (species combined). For summer data, mean density was the dependent variable and macrohabitat and year were independent variables. For autumn data, mean density was the dependent variable, and macrohabitat, year, and site were the independent variables. All data were log transformed to meet normality assumptions. It is important to note that significant differences between mean densities in any two macrohabitats were indicated by ANOVA only when those differences occurred throughout all years. When significant differences were detected by ANOVA, we used a Least Squares Means Probability Difference Analysis (LSMPDA) to determine where differences occurred (SAS Institute, Inc., 1989) We used an alpha level of $P = 0.05$.

We performed a power analysis on Jacks Fork River data to estimate the ability of our quadrat sampler and our method to assess the probability of Type II error in detecting differences in crayfish densities among macrohabitats (Somers, 1997). Also, we determined power to detect temporal density differences within macrohabitats among 5 y of sampling (sampling every year) and also among only 3 y of sampling (every other year) within a 5-y period. This was done to gain insight into appropriate sampling frequencies that might be required to monitor and effectively detect density changes in stream crayfish communities.

Table 1. Descriptions of five macrohabitats used to stratify sampling effort in Jacks Fork and Big Piney rivers, Missouri, U.S.A. Water depth and current velocity (CV) are 95% confidence limits for both rivers.

Macrohabitat type	Relative (%) composition[a]	Depth (m)	CV ($m \cdot s^{-1}$)[b]	Qualitative description
Riffle	7–15	0.17–0.22	0.14–0.24	Notable surface turbulence
Run	26–42	0.32–0.40	0.06–0.12	Minimal surface turbulence
Pool	44–57	0.40–1.16	0.02–0.04	No surface turbulence
Backwater[c]	1–4	0.18–0.31	0.00–0.01	Partially isolated from channel
Vegetation patch[d]	2–9	0.16–0.23	0.01–0.04	On stream margin

[a] Values are a range derived from two intensive mappings of all sites in two different years.
[b] Current velocities were recorded 2 cm above substrate, where crayfish were most affected.
[c] Backwaters also included forewater and side channel pools, and often were ephemeral.
[d] Vegetation patches were emergent aquatic vegetation patches comprised of water willow, *Justicia* sp.

RESULTS

Sample Stratification Method

Mean crayfish densities in marginal habitats of Jacks Fork and Big Piney rivers were $0.9 \cdot m^{-2}$ (SE $\pm$ 0.2, $n = 65$ samples in June and $n = 18$ samples in August). Crayfishes were absent from 67% of samples.

The DFA performed to quantify our distinction between primary and marginal habitat yielded significant discriminant functions for all study sites (details provided in DiStefano, 2000) and validated our first level of stratification in field sampling. The Jacks Fork River classification rule classified 97% (36 of 37) of our marginal habitat samples correctly and 94% (1077 of 1142) of our primary habitat samples correctly. The Big Piney River classification rule classified 96% (44 of 46) of our marginal habitat samples correctly and 98% (803 of 819) of primary habitat samples correctly.

Crayfish Macrohabitat Associations

We detected spatial and temporal differences among diurnal mean crayfish densities and observed that crayfishes were using many of the available habitats within our study streams. Mean crayfish densities differed spatially among the five macrohabitats across all years during summer in both rivers and during autumn in Jacks Fork River (Table 2) and differed spatially between the two sites at Big Piney River ($P < 0.0001$). Densities also differed temporally within macrohabitats ($P < 0.05$) among years at both rivers during both seasons. Crayfish densities decreased among three of the five macrohabitats across a 5-y period, but not for a 3-y period at Jacks Fork River (Tables 3, 4). Significant 2-way and 3-way interactions occurred in the ANOVAs for Jacks Fork River autumn data and Big Piney River summer data, but they were ordered, as indicated by the lack of crossover when least square means were plotted, and they masked no main effects (Table 2; Ott, 1988).

During summer at Jacks Fork River, backwaters, vegetation patches, and pools yielded significantly higher mean crayfish (*Orconectes luteus*, *O. ozarkae*, and *O. punctimanus* combined) densities (about $30 \cdot m^{-2}$) than runs and

Table 2. Results of 2-way (summer data) and 3-way (autumn data) ANOVAs and LSMPDAs comparing crayfish mean densities among macrohabitats in Jacks Fork and Big Piney rivers, Missouri, U.S.A., 1991–1998.

	ANOVA statistics			
	F	*df*	*MSE*	*P*
Jacks Fork — summer				
Macrohabitat	20.5	4,300	0.5024	< 0.0001
Year	9.06	4,300		< 0.001
Macrohabitat * year	0.87	16,300		0.6081
Jacks Fork — autumn[a]				
Macrohabitat	32.55	4,361	0.3403	< 0.0001
Year	7.07	2,361		0.001
Macrohabitat * year * site	2.81	8,361		0.0049
Big Piney — summer[b]				
Macrohabitat	45.88	4,288	0.4061	< 0.0001
Year	2.02	4,288		0.0913
Macrohabitat * year	1.78	16,288		0.0330
Big Piney — autumn[c]				
Macrohabitat	2.68	2,144	0.4054	0.0721
Year	5.18	1,144		0.0243
Macrohabitat * year * site	0.90	2,144		0.4071

[a] Jacks Fork River, macrohabitat * year * site interaction was significant, but ordered (Ott, 1988). LSMPDA showed vegetation patches differed from riffles ($P < 0.0001$) and runs ($P < 0.0001$); riffles differed from backwaters ($P < 0.0001$) and pools ($P < 0.0001$).
[b] Big Piney River, macrohabitat * year interaction was significant ($P = 0.0330$), but ordered (Ott, 1988). LSMPDA showed vegetation patches and backwaters differed from all other macrohabitats (all comparisons, $P < 0.0001$); pools differed from riffles ($P = 0.0084$).
[c] The analyses for Big Piney River autumn sampling included only the macrohabitats riffles, runs and pools; all data for backwaters and vegetation patches were excluded because of a lack of those samples in 1993.

Table 3. Statistical power of comparisons of mean crayfish densities (number · m^{-2}) using five years of data from Jacks Fork River, Missouri, U.S.A. Column on far right represents statistical power of comparisons within a macrohabitat across years; row on bottom represents power of comparisons within years across macrohabitats.

	Mean density						
Macrohabitat	1994	1995	1996	1997	1998	*P*-value	Power
Riffle	20.5	11.4	13.1	7.4	10.9	0.0393	0.43
Run	34.7	27.8	21.3	10.4	14.0	< 0.0001	0.97
Pool	42.9	37.9	26.6	21.0	24.6	0.0021	0.85
Vegetation	43.4	40.0	30.0	23.0	35.0	0.3889	0.00[a]
Backwater	45.8	55.8	38.4	28.6	17.4	0.2557	< 0.38
P-value	0.2760	< 0.0001	0.0004	0.0064	0.0041		
Power	< 0.38	0.99	0.96	0.78	0.80		

[a] Power value of 0.00 achieved when the mean square of the error term equals the mean square of the model term (Somers, 1997).

riffles across all years (Fig. 3). Densities in riffles (13 · m^{-2}) were significantly lower than those in all other macrohabitats. Coefficients of variation among the five macrohabitats for each year (1994–1998) during summer at Jacks Fork River ($n = 25$ coefficients of variation) ranged from 31% to 90%, with a median of 59%.

A similar pattern was observed during autumn at Jacks Fork River (Fig. 3). Vegetation patches yielded significantly higher densities (42 · m^{-2}) than runs (22 · m^{-2}) and riffles (17 · m^{-2}) across all years. Riffle densities were lower than all other macrohabitats. Coefficients of variation ranged from 9% to 78% with a median of 47% ($n = 30$).

During summer at Big Piney River, backwaters (52 · m^{-2}) and vegetation patches (44 · m^{-2}) produced significantly higher densities of the two crayfishes (*O. luteus* and *O. punctimanus* combined) than all other macrohabitats (Fig. 3). Densities in pools (16 · m^{-2}) were higher than in riffles (13 · m^{-2}). Coefficients of variation among macrohabitats ranged from 31% to 99% with a median of 58% ($n = 25$).

Mean crayfish density patterns among macrohabitats for Big Piney River autumn sampling appeared similar to summer data; vegetation patches (27 · m^{-2}) and backwaters (26 · m^{-2}) yielded high densities relative to the other three macrohabitats (10 to 14 · m^{-2}, Fig. 3). However, a lack of samples from vegetation patches and backwaters in autumn of 1993 (because of floods) precluded inclusion of those macrohabitats in the corresponding ANOVA and masked possible differences among all macrohabitats. Coefficients of variation ranged from 31% to 105% with a median of 54% ($n = 12$).

Power Analysis

Our sampling produced sufficient power to detect spatial crayfish density differences among macrohabitats, but less power to detect temporal (among year) differences within macrohabitats. Power to detect density differences among macrohabitats was 78% or greater in 4 of the 5 y tested (Table 3, bottom row). Power to detect density differences among years was variable, but it was best in run and pool macrohabitats (Table 3, far right column) where mean densities were significantly different among years (Table 3, second column from right). Power was higher when we sampled and analyzed data each year in a 5-y period (Table 3, far right column) than if sampling had occurred only every other year (3 y) during that period (Table 4, far right column). Power was predictably highest among

Table 4. Statistical power of comparisons of mean crayfish densities (number · m^{-2}) using three years of data from Jacks Fork River, Missouri, U.S.A. Column on far right represents statistical power of comparisons within a macrohabitat across years.

	Mean density				
Macrohabitat	1994	1996	1998	*P*-value	Power
Riffle	17.1	12.6	9.3	0.0677	0.40
Run	26.9	19.0	13.8	0.2314	0.20
Pool	34.5	26.8	23.4	0.1326	0.30
Vegetation	35.6	30.5	33.3	0.7702	N/A[a]
Backwater	35.0	31.4	23.9	0.3595	0.00[b]

[a] Mean square error term was greater than the mean square of the model term, producing a negative phi value (Somers, 1997).
[b] Power value of 0.00 achieved when the mean square of the error term equals the mean square of the model term (Somers, 1997).

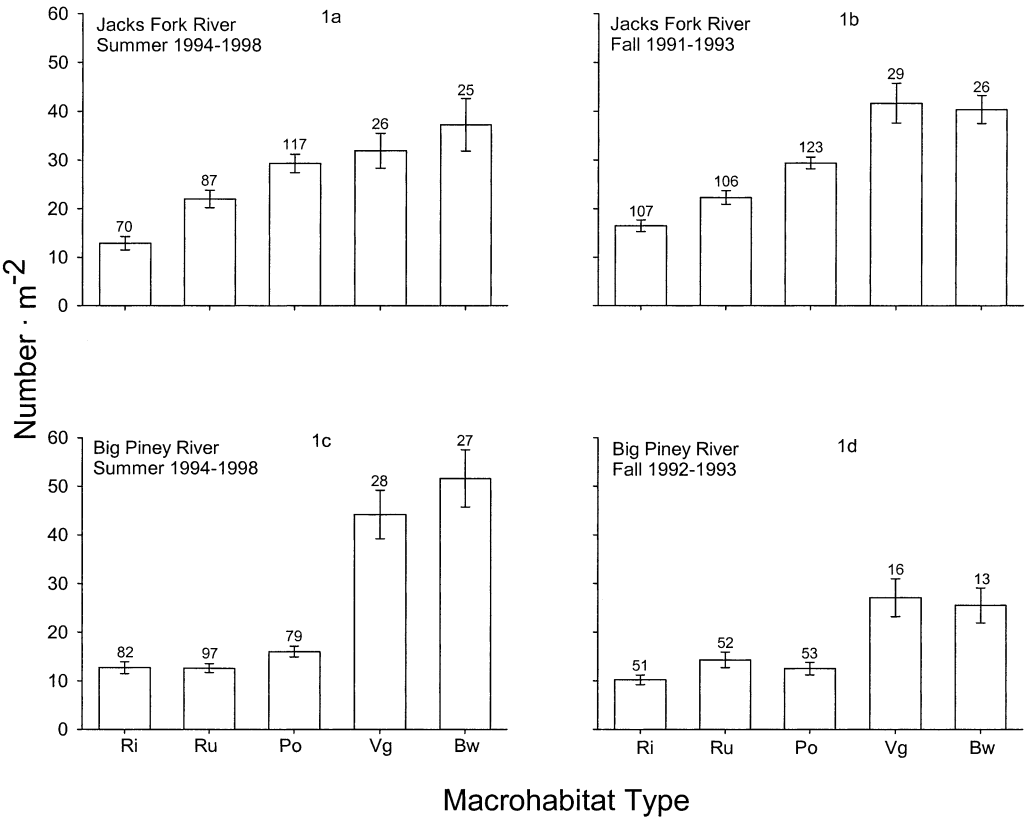

Fig. 3. Crayfish community mean densities (number · m^{-2}) among macrohabitat types (Ri = riffles, Ru = runs, Po = pools, Vg = emergent vegetation patches, Bw = backwaters) at Jacks Fork (JF) and Big Piney (BP) rivers, Missouri, U.S.A. Error bars represent ± 1 SE. Sample sizes (number of 1-m^2 quadrats, N) appear above bars. 1a) JF summer densities in riffles were significantly ($P < 0.05$) lower than those in all other macrohabitats across all years. JF summer densities in runs were significantly lower than those in pools, vegetation and backwaters across all years. 1b) JF autumn densities in vegetation patches were significantly higher than those in riffles and runs across all years. JF autumn densities in pools and backwaters were significantly higher than those in riffles across all years. 1c) BP summer densities in vegetation patches and backwaters were significantly higher than those in all other macrohabitats across all years. BP summer densities in pools were significantly higher than those in riffles across all years. 1d) A lack of autumn samples from vegetation patches and backwaters at BP site 2 in 1993 precluded inclusion of those macrohabitats in the ANOVA for both sites and both years. ANOVA featuring riffle, run and pool macrohabitats yielded no significant differences among those macrohabitats.

groups of mean densities that were the most variable (i.e., had the greatest "effect size").

Discussion

Quantitative Sampling Method

Many aspects of research and management of lotic crayfishes require a reliable and efficient quantitative method to sample and evaluate populations and communities. However, there has been limited work to develop such methods (Westman *et al.*, 1978; Rabeni *et al.*, 1997; Byrne *et al.*, 1999). Several investigators have reported densities of lotic crayfishes (see reviews in Momot *et al.*, 1978; Hogger, 1988; DiStefano, 1993), but few of these evaluated the reliability of their sampling method, and stratification by habitat was uncommon. Our major objective was to develop a method to obtain representative and precise stream crayfish diurnal density estimates that could be used for spatial and temporal comparisons, and to illustrate the method's value by describing 1) general habitat associations by stream crayfish communities, including crayfish density differences among those habitats; and 2) density changes within macrohabitats over time. Our method performed well, but was not without problems.

The 1-m^2 quadrat sampler was effective for sampling crayfish communities in Jacks Fork and Big Piney rivers. This sampler provided several advantages including a known area for

density estimates. Because good visibility was not required, the sampler could be used in turbid streams. The high enclosed sides and the bottom flaps that seal into the substrate addressed problems associated with seines and open-sided known-area samplers (e.g., Surber sampler) such as escapement, immigration of organisms from outside the sample area, and decreased effectiveness in minimal current (Bretschko, 1990; Brooks, 1994). The 1-m^2 quadrat sampler also had limitations. In deep waters, we attempted to restrict crayfish escape over the top of the sampler but were not always successful. We could not sample substrates greater than 1 m in diameter (large boulders) or crevices in the limestone bluff walls that are characteristic of many streams in our region of the world. Many of the largest crayfish (age 2 and perhaps 3) in these streams use these habitats and thus were underestimated in our samples. However, they compose a relatively small part of the crayfish community (Muck, 1996).

The first step of our quadrat sampling procedure, delineating primary and marginal habitat, was appropriate for both rivers, as suggested by the high classification rates produced in the DFA. However, our classification rates were optimistically biased because we used the same data to define and evaluate the classification rules (Dillon and Goldstein, 1984). Despite the bias, the high classification rates suggest that our stratification method was repeatable and allowed us to distinguish effectively primary from marginal habitats. Marginal habitats made up a relatively small portion of our streams, but had we not stratified at this level, and thus obtained samples in those areas, crayfishes would likely have been absent from most (67%) of those samples. Addition to the database of significant numbers of samples containing zero observations would not conform to our chosen analysis techniques based on normal distributions (Downing, 1989). The potential effects of samples containing zero crayfish are not fully known, but they could further increase variability depending upon crayfish densities in the remainder of our samples. If investigators were primarily interested in obtaining whole-stream abundance estimates, they might consider sampling marginal habitats but might do so at the expense of precision. These are important issues to be considered by others who engage in quantitative sampling of lotic crayfish communities.

The second step of our procedure, stratifying quadrat sampling among five macrohabitats, partially mitigates the higher variance normally associated with simple random sampling of organisms that exhibit spatial heterogeneity (Morin, 1985; Thompson *et al.*, 1992). Stratification by macrohabitat facilitated detection of temporal (among years) differences and was essential for detection of spatial (among macrohabitats and sites) differences in crayfish densities. For example, had we not collected separate data for riffles and runs, we would have failed to learn that crayfish densities differed between those two macrohabitats in Jacks Fork River during summer (Fig. 3), we would not have detected differences between riffle densities and densities in pools and backwaters in Jacks Fork River during autumn (Fig. 3), and we would not have detected differences between riffles and pools in Big Piney River during summer (Fig. 3). Failure to stratify our sampling by macrohabitat also would have decreased our capacity for detecting temporal density changes in those macrohabitats.

Our sampling precision, as measured by coefficients of variation, was not high, but acceptable relative to published values from a similar study by Roell and Orth (1992). Precision also was variable among spatial and temporal components of the analysis. Precision of mean densities in sampling for freshwater benthic invertebrates tends to vary with and is affected by magnitude of the mean, the physical size of the sample (quadrat size), and the number of samples (Morin, 1985; Cooper *et al.*, 1997); only the latter two factors can be controlled and thus modified to improve precision. Prior to the study, we debated the size of our quadrat sampler. A smaller quadrat would have been easier to manipulate, but would have excluded sampling in some larger substrates (particularly large cobble and small boulder), and smaller sampling units typically lead to higher variance (Morin, 1985). We believed that a quadrat much larger than 1 m^2 would be unwieldy and impractical. Lamontagne and Rasmussen (1993) required fewer samples with a 10-m^2 quadrat sampler to obtain similar crayfish densities as a 1-m^2 sampler in northern lakes; but the smaller sampler was more efficient at densities above $0.3 \cdot m^{-2}$ because it required less overall effort. Our sample sizes were constrained by our desire to sample multiple sites and sampling periods and by the number of available personnel. However, our experience taught us that spatial and temporal differences in crayfish

density data can be detected using quadrat sampling with intensive effort.

Precision associated with our crayfish sampling method was less than might be desired for some studies but could be misleading because small coefficients of variation can be produced even with highly biased sampling methods (Rabeni *et al*., 1997). We could have improved precision slightly in some macrohabitats by increasing sample size. However, a sample-size determination analysis for *O. luteus* in Jacks Fork River indicated that increased sampling (beyond about 12 samples) of riffle or run macrohabitats would not have significantly improved precision of density estimates, suggesting that we were not grossly undersampling (DiStefano, 2000). Precision was not the only important variable considered in our evaluation. Future stream crayfish sampling efforts will probably be designed to detect potential changes or differences in densities or population levels attributed to predators, pollutants, physical habitat changes, or invasive species. Good statistical power is as important as precision in such sampling efforts (Downing and Downing, 1992) as it assesses the ability of a study to detect changes or differences when they truly exist (Somers, 1997). A standard criterion for power has not been developed (Somers, 1997), but based on our analyses, we rate this quadrat sampling method's power to detect spatial differences (78% or greater in 4 of 5 y) as good. Seventy-eight percent power implies a 22% chance of Type II error, or that about four out of five statistically significant effects were detected in those years. Power to detect temporal changes was very low when only 3 out of 5 y of sampling data were analyzed (Table 4), but increased to acceptable levels in two of the five macrohabitats when all 5 y of data were used (Table 3). This suggests that we could detect temporal changes among the five macrohabitats if we increased the length of study and sampled every year. These results also confirm the importance of evaluating statistical power of sampling programs designed to detect temporal population or community changes, a practice that is often disregarded in freshwater benthic studies. Our power was a function of the size of mean crayfish densities, the effect size (or difference among those means), sample size and the alpha level of $P = 0.05$. In future sampling, we could increase power to detect spatial or temporal differences by decreasing the amount of error associated with each sample (thereby increasing the relative effect size), increasing the number of quadrat samples allocated among the macrohabitats, or decreasing the alpha level (Somers, 1997).

An additional concern with most sampling methods is the potential for operator-induced error. Stream benthic sampling methods have been shown to be susceptible to variation associated with different operators (Pollard, 1981), but methods that employ box-type quantitative samplers, like our quadrat, are probably less susceptible than many qualitative methods (Clifford and Casey, 1992). We believe we minimized such bias by extensively training field crews and using a standardized procedure.

This quantitative quadrat sampling method allowed us to document the influence of habitat on crayfish community distributions in Jacks Fork and Big Piney rivers. We were impressed by the general consistency of macrohabitat use across rivers and seasons. Macrohabitats with slower current velocities generally had highest crayfish densities, although many factors other than current velocity probably contributed. Consistently high crayfish densities in backwaters and vegetation patches indicated their importance as habitats despite their relatively sparse distribution (1–4% and 2–9% of the total stream habitat, respectively; Table 1). This reinforced our belief that the crayfish communities of these two streams are not distributed randomly, but exhibit macrohabitat selectivity (Flinders, 2000). Our observations were facilitated by stratification of samples among all five macrohabitats. There are several published studies documenting lotic crayfish habitat associations or use as quantitatively measured by densities or abundance (Vannote and Ball, 1972; Butler and Stein, 1985; Rabeni, 1985; Mitchell and Smock, 1991; Roell and Orth, 1992; Creed, 1994; Muck, 1996; Peterson *et al*., 1996; Englund and Krupa, 2000; Flinders 2000). To our knowledge none of these studies or any others documenting densities/abundance of lotic crayfishes (Mason, 1963; Brown and Bowler, 1977; Brown and Brewis, 1978; Westman *et al*., 1978; Brewis and Bowler, 1983; Taylor, 1988; Stelzer and Burton, 1993; Guerra and Niño, 1995; Richards *et al*., 1996; Rabeni *et al*., 1997; Byrne *et al*., 1999; Grandjean *et al*., 2000), were as intensive over an extended period of time as this study. Only Peterson *et al.* (1996) sampled for more than 2 y (3 y in their case). Mitchell and Smock (1991) measured crayfish densities on six substrate size classes, but did not delineate

specific macrohabitats. Only Muck (1996) and Flinders (2000) thoroughly examined crayfish densities in more than three macrohabitats (five and six, respectively). Their studies, like ours, were conducted in Ozarks streams and reported higher crayfish densities in emergent vegetation and backwaters than in riffles and runs. Flinders' (2000) work also produced evidence to suggest that a sixth macrohabitat might be appropriate for inclusion in future studies depending upon the composition of individual streams. Shallow (< 0.15 m depth) "edgewaters" (DiStefano, 2000) or "stream margins" (Flinders, 2000) with slower current velocities (< 0.03 m $\cdot$ s^{-1}) and potentially warmer temperatures can harbor crayfish species, size classes and/or densities that are distinctly different from other macrohabitats (DiStefano, 2000; Flinders, 2000).

Conclusions

Our initial goal was to develop a quantitative sampling method that would help us assess the status of lotic crayfish communities. The 1-m^2 quadrat sampler proved effective for sampling most of the crayfish community in these streams during summer and autumn, and the quantitative sampling method performed well in estimating crayfish densities in the five macrohabitats and detecting spatial density differences and some temporal differences among them. The quadrat proved less effective (reduced precision; DiStefano, 2000) in spring because of the timing of hatching in these *Orconectes* species. It is important to incorporate life history events and their potential effects on availability or susceptibility of biota to sampling when planning a study (Rabeni, 1996), and many invertebrate community studies ignore such considerations (Malley and Reynolds, 1979). It is also necessary to design the sampling method to conform to the physical constraints of the study stream because no single method is appropriate for every situation (Rabeni *et al*., 1997). Our method was developed and tailored specifically for use in a relatively common aquatic situation, small to medium-sized streams with rocky substrate. Our intent was not to develop nor prescribe a method with complete applicability, nor necessarily to provide crayfish density data for comparison with other communities. However, given the relative absence of published, reliable methods for quantitatively sampling lotic crayfish populations or communities, this method, or parts of it, may prove valuable to investigators in other regions of the world. Downing and Downing (1992) reported that 85% of published density estimates of benthic invertebrates were based on only three or fewer samples. Our method is considerably more labor and time intensive, but it reduces a substantial amount of variability and provides more confidence in density estimates of stream-dwelling crayfishes than other sampling methods such as trapping (Brown and Brewis, 1978; DiStefano, 2000), and direct observation (Rabeni *et al*., 1997). Because it can be used in combination with snorkeling or SCUBA, the quadrat method is applicable in a wider range of water depths than methods such as electrofishing and seining. Future efforts could include modifications to improve performance detecting temporal changes in crayfish densities and possibly to sample effectively all segments of the community. Such modifications might include increasing statistical power by increasing sample size, or incorporating a second sampling technique (Malley and Reynolds, 1979), to obtain quantitative data on the oldest age class(es), although we believe that segment of the crayfish community in these Ozarks streams is very small (Muck, 1996).

Crayfish biologists rarely have the opportunity to allocate several years and significant resources toward developing and evaluating sampling gears and methods. Despite that luxury, the method we developed was not without problems. Throughout this study no single sampler or method was best suited for every situation, even within the same water body. In addition, our experience reaffirmed that quantitative community studies should incorporate pilot studies and sufficient time for evaluation of samplers and methods. For example, we performed a pilot evaluation on the use of baited traps because of their unknown potential for use in streams and because they have been used in lentic waters to produce reliable estimates of crayfish relative abundance (Capelli and Magnuson, 1983; Collins *et al*., 1983; Olsen *et al*., 1991; Skurdal *et al*., 1992; Somers and Green, 1993; Acosta and Perry, 2000), despite known size, sex, and seasonal biases. However, we found that, for several reasons (size and sex biases, high sampling variance, many empty traps, theft, and violation of equal probability of capture due to variation in dispersal of bait odor), baited traps were not acceptable for quantitative sampling of lotic crayfishes (DiStefano, 2000).

Despite our use of two notably different Ozarks streams, the 1-m^2 quadrat sampling method demonstrated that the crayfish communities were similar in that they used a variety of habitats in a similar pattern. While these patterns

remained consistent over several years, densities within distinct macrohabitat types showed significant interannual variation. Macrohabitats featuring emergent vegetation patches and shallow backwater pools consistently harbored the highest diurnal crayfish densities, whereas riffles held the lowest. Future work will employ the 1-m^2 quadrat sampling method to study how crayfish species and age classes in these communities partition available habitats and to examine how crayfish production is allocated among the macrohabitats.

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